

THE CARDINAL PRINCIPLES OF MORPHOLOGY.²

ALTHOUGH botany has made remarkable advances in America during the past few years, there is still one phase in which it remains singularly backward, namely, in its treatment of the morphology of the higher plants. There still prevails among us, with little modification, the old formal idealistic morphology, whose founder was Goethe, and whose great exponent in this country was Gray; while we give scant consideration to the newer natural realistic system, now more or less fully accepted elsewhere, and recently given greater extension by its leading advocate, Goebel. We have, it is true, some literature of the newer morphology, of which an example is Professor Barnes' discussion of the Flower in the *Cyclopedia of American Horticulture*, while the treatment of the homologies of the higher with the lower plants is good in most of our recent text-books; but from these there is every gradation backward. Happily the newer standpoint is becoming generally accessible to American students through the publication of Goebel's *Organographie der Pflanzen* (Jena, Fischer, 1898-1900), now being translated into English under the title *Organography of Plants* (Part I, Oxford, Clarendon Press, 1900). In the present paper I propose to summarize what seem to me the principles upon which the newer morphology is based.

The difference between the idealistic and the realistic morphology, while partly one of fact, is mainly one of point of view. The idealistic system is based principally upon comparative anatomy; it concentrates attention upon the steps, or stages, in morphological changes, or metamorphoses, but is largely indifferent as to the processes, or mechanics, by which the metamorphoses have been brought about; metamorphosis is therefore to it chiefly a phylogenetic operation, whose exact ontogenetic basis is of secondary consequence. The realistic system, while giving great weight to comparative anatomy, lays especial emphasis upon the testimony of embryology, particularly seeking the actual ontogenetic origin and development, the mechanics, of metamorphoses, only through which, it maintains, can the true nature of metamorphosis be understood; metamorphosis is, therefore, to it primarily an ontogenetic process which later and secondarily becomes fixed in the phylogeny. The former, the idealistic or phylogenetic system, predisposes one to generalized and abstract conceptions, while the latter, the realistic or

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ontogenetic, leads to more definite and concrete conclusions. Both views equally assume the fact of evolution in the phylogenetic fixation of metamorphoses, but both are equally independent of the exact method (the dynamics) by which that evolution is brought about, whether this be through natural selection involving the whole organism, or through germinal selection, or through organic selection, or through the accumulation of transmitted effects of individual irritable responses, or through some other method still unknown. The realistic system, however, brings us more nearly face to face with the problems of the dynamics of evolution than does the idealistic system.

We pass next to an attempt to deduce the fundamental or cardinal principles of morphology. Of these, some are not peculiar to morphology alone, but belong equally to other phases of evolution and adaptation, while others are especially characteristic of morphology.

FIRST, the principle of *continuity of origin*, that is, no functional structure ever arises *de novo*, but only from the modification of a pre-existing structure, which in turn arose from a still earlier, and so on backward through a longer or shorter chain ending only in the original protoplasmic variation, or in whatever it is which does lie at the beginning of specialization. This principle is axiomatic for both systems of morphology.

SECOND, the principle of *opportunism*, that is, the direction taken in metamorphosis is not determined by obedience to any pre-formed plan, but, except for the influence of the inertia of the heredity of the particular part, follows the factors potent at the moment. Heredity of itself cannot impose any plan, for it is but the summation of the interaction of past experiences with original properties. Theoretically this principle should be as acceptable to the idealistic as to the realistic morphology. In practice, however, the idealistic conception of metamorphosis as a whole is that of a play of a very few highly plastic "members," which, however much they may vary and combine, retain a sort of fundamental immutability of nature, as witness the efforts to explain all parts of the flower in terms of "leaves" and "stem," and the use of the expression "disguised" often applied to metamorphosed parts. There is thus imposed upon metamorphosis a sort of ideal plan, a plan implying that modification keeps within certain limits, determined by the possibilities of permutations and combinations of those members. The realistic morphology is bound by no such conception,

for the members are unlimited in number and have no ideal nature or limitations to be consulted.

THIRD, the principal of *functional domination* in metamorphosis, that is, it is function which takes the lead and structure follows. It is of course true that function and structure are reciprocally related; there are cases where structure determines function; there are other cases in which non-functional factors, especially an aggregation of them, may outweigh a functional factor; nevertheless, it must be true that in a broad way it is function which determines structure, function often hampered, and even sometimes thwarted by other influences it is true, but function dominant in the long run. If this is not true, adaptation is but an accident if not a myth, and our whole idea of it but a vain vamping of the imagination. This principle in general is necessary to both systems of morphology, but it is more prominent in realistic than in idealistic discussions.

FOURTH, the principle of *indeterminate anatomical plasticity*, that is, in all anatomical characters (size, shape, number, position, color, cellular texture) plant-organs, or, if one pleases, plant-members, are not limited by anything in their morphological nature, but, under proper influence, may be led to wax and wane indefinitely in any of these respects. Of course this plasticity is hampered by innumerable practical considerations, and by many hereditary "tendencies," and many generations may be (though they are by no means always) necessary to produce a marked and permanent result; but the point is that limitations to anatomical plasticity do not come from the morphological nature of the part concerned. The principle may also be stated thus, that there is no causal relationship whatever between morphological nature and anatomical structure; stipules are usually smaller than the leaves they accompany and markedly different in form; yet they may become as large as the leaves and indistinguishable from them (as in *Galium*), or much larger, as in some Leguminosae; there is obviously therefore nothing in the nature of a stipule as such to limit its size or shape; that it is usually smaller than its leaf is a purely functional and non-morphological matter. So, stems may lengthen immensely as in climbers or shorten to apparent disappearance as in rosette-plants, and so on with all other parts. This principle is equally true for both systems of morphology, and is perhaps the most clearly recognized of them all.

FIFTH, the principle of *metamorphosis along lines of least resistance*,

closely related to opportunism mentioned above. This means that when, through a change in some condition of the environment, the necessity arises for the performance of a new function, it will be assumed by the part which happens at the moment to be most available for that purpose, regardless of its morphological nature, either because that part happens to have already a structure most nearly answering to the demands of the new function, or because it happens to be set free from its former function by change of habit, or because of some other non-morphological reason. It is due to the operation of this principle that structures of the most different morphological origin may come to serve the same function, and correlatively, structures of the same morphological origin may come to serve the most different uses. The genus *Pereskia*, in the Cactaceae, includes mesophytic climbers with true broad leaves, from which all gradations in reduction of leaves and condensation of stem may be traced even to the typical desert forms of *Cereus*. Now, one division of *Cereus* returns to a life in the woods, where the demand for an increase of green surface is felt; no attempt, however, is made to restore the old leaves (now reduced to tiny scales), but the stem enlarges and branches, while the vertical ribs, developed during the desert habit, are expanded farther and made to function as leaves. As the mesophytic habit becomes more extreme, the ribs become larger in size and fewer in number until finally, in *Phyllocactus*, but two remain, and these become so flattened and arranged in such a manner on the branch that they form a physiological and anatomical leaf. Here we have a case, indubitable because abundant intermediate steps persist, in which a physiological leaf has been developed from a morphological stem, purely by following the line of easiest accomplishment, or least resistance, at the moment; no single step is in itself remarkable, but the sum total yields a very remarkable result. This principle is, of course, equally applicable to both systems of morphology.

SIXTH, the principle of *metamorphosis by transformation*, as contrasted with *metamorphosis by differentiation*, which means that when, in response to any influence, a new function and hence structure (function-structure) is assumed by any part, this always comes about, both ontogenetically and phylogenetically, through the transformation or alteration of a previously existing function-structure in that part, and never through the differentiation of a new function-structure out of a previously functionally-indifferent or unspecialized structure. In

other words, since all parts of the plant actually are organs (that is have some meaning in the life of the plant), new organs can arise only by the transformation of previously existing ones. We face here a sharp contrast in the two systems of morphology. The idealistic system, laying as it does great stress upon members in distinction from organs, comes to regard these members as if they had a real existence, forgetting that the conception of the member is a pure abstraction of the mind, a sort of mental composite photograph, with no objective equivalent, and that members apart from organs do not really exist. The conception of the member as an entity having once been formed, metamorphosis is naturally regarded as the differentiation of an organ out of a member, and this not only phylogenetically but also ontogenetically; so that by those who carry the idealistic system into ontogeny at all, the ontogenetic unfolding of any organ is viewed as a differentiation from primordia (Anlagen) which, after the analogy of the members, are supposed to be indifferent in their nature. Not only, however, is this view untenable upon philosophical grounds, but it is negated by the fact that in cases where metamorphoses are experimentally brought about, embryology shows that the process is actually one of transformation of one function-structure into another, and not of differentiation of a function-structure out of a neutral or indifferent primordium (Anlage). But this subject is so clearly treated by Goebel in the Introduction to his *Organography* that it needs no further consideration here. How these, in their origin purely ontogenetic, metamorphoses become fixed in the phylogeny, is an entirely separate question, the solution or non-solution of which does not in the least affect the truth or non-truth of this principle. The idealistic conception, that an organ is formed by differentiation from a member, implies as a corollary that each organ is but one step, so to speak, from a member, and should be readily reducible to it; hence arise the attempts to explain all parts of such complex and specialized structures as epigynous flowers in terms of leaf and stem, necessitating the adnate calyx theory with its requirement of extraordinary assumptions as to growing together of parts, etc., entirely unsupported by the facts of development.

SEVENTH, the principle of *gradation in morphological membership*, involving the existence of degrees of morphological independence, culminating in the attainment of full morphological membership with full independence. Or, it may be expressed thus: in the progressive

development of metamorphoses, difference of degree passes over gradually into difference of kind. This principle, in my opinion the most fundamental in morphology, marks far more sharply than any other the difference between the two systems, for it is fundamental to the realistic, but inconsistent with the idealistic conception. It means that, as an organ gradually acquires a new function-structure, and the old function-structure is gradually lost, new powers of variation, adaptation, etc., are acquired which become more and more independent of those formerly possessed by the organ, until finally the change may become so complete that the new organ not only acts itself quite independently of its old nature, but becomes a new starting point or center of metamorphosis, that is, it becomes a new morphological member. New metamorphoses, however, are not confined for their starting-point to the full members, but may originate from any of the points along the lines of gradation. Hence, not only may any organ become a member, but the members grade into one another indefinitely and any of the gradations may act as members. This is in great contrast with the conception of the idealistic system as applied to the higher plants, for that conception not only limits the number of the members to a very few (at the extreme root, stem, leaf, plant hair, exclusive of the sporangia), but practically views these as sharply distinct, not recognizing intermediate transition from which new metamorphoses may originate. In fact the idealistic morphology, while admitting the original evolutionary origin of its members, ignores evolution in their subsequent interrelationships; it views its members much as species were viewed in pre-evolutionary times, while the realistic system applies the idea of evolution throughout. The idealistic system views the morphological members much as a chemist does his elements, which may combine in many ways, but retain their identity throughout; the realistic system regards them more as a physicist does the colors of a spectrum, as a series of stages in a graded sequence of phenomena.

As an example of an organ which has attained to full morphological membership and independence we may consider the spines in the Cactaceae. Research has shown much evidence for the belief that these structures have arisen by the metamorphosis of leaves; the only competing theory is that they are a form of "emergences;" no investigator has ever seriously supposed they were anything else. Now, despite much long-continued observation and special search, no one has ever

been able to find transitions between these spines and either leaves or emergences (except in the case of a few monstrosities which may have another meaning), nor have repeated experiments succeeded in making the spines return to leaves or emergences. Now, the cactus spines are immensely variable, becoming very big and hard on the one hand, or weak and small even to disappearance on the other, cylindrical and erect to ribbon-like and contorted, plain or variously ornamented, smooth or beautifully plumed or fringed, curved into hooks useful for climbing, or altered entirely into nectaries. But, throughout all of these variations it is distinctly and unquestionably a spine, an anatomical spine that is varying, and not a disguised leaf or emergence. We must conclude from all these grounds that the cactus spine has attained to full morphological membership, is itself a member, a center of modification and metamorphosis. The mamillae, or tubercles, in the same family, originate by a union of the leaf-base and its axillary bud, but the identity of these two parts becomes completely lost in the new identity of the tubercle, which becomes a member and acts as such through many genera. The ribs in Cactaceae arise by the running together of vertical lines of tubercles; once formed, however, they pay little attention to their mode of origin but proceed to act as independent members, as one may clearly see when he considers their performances (particularly their independent increase or reduction in number) in the development of the cladophylls of *Phyllocactus* already cited in this paper. In some genera, however, particularly *Echinocactus*, the ribs have not attained to full independence, for they occasionally revert to lines of tubercles. But we need not go so far afield for our illustrations of the attainment of independent membership, for the members commonly accepted by the idealistic system (root, stem, and leaf) illustrate it perfectly. Most of us no doubt believe that the present-day foliage leaf and stem arose through the sterilization of sporogenous tissue in a primitive very simple sporophyte; but whether we believe it or not does not matter for our present purpose, for we must believe, if we accept evolution at all, that leaf and stem have become specialized out of a simpler structure which did not show those distinct parts. All morphologists accept the foliage leaf and its stem as of full morphological membership and independence, to such a degree indeed that they stand in most minds as the very types of morphological members. Now, in their case, even the idealists never attempt to interpret their morphological behavior in the light of the nature they

had before they were leaf and stem. Why, then, does the idealistic morphology insist, for example, upon reducing everything (excepting the sporangia) in a highly specialized flower to the categories of leaf and stem? In fact, the flower has been so long an independent organ that it has had time to progress far toward independent morphological membership, as witness its ability to suppress circles, to alter the number of their parts, and to rearrange their phyllotaxy quite independently of any actions performed by leaves on a stem. Moreover, various parts of the flower (in some flowers, not in all) have become more or less independent members, as we may clearly see in those which are epigynous. The ovary of such a flower, for example, unquestionably originated in sporophyllary leaves standing upon a conical receptacle, precisely as in numberless flowers today; gradually, however, as embryology proves, the formation of the ovarian cavity was given up by the carpels, and assumed by the receptacle, which grew up in the form of a cup carrying the other parts upon its rim, while the carpels finally came to form simply a roof over the cavity. But, and here is a crucial point, it must not be supposed that during this process the receptacle and carpels retained their old carpel and receptacle nature (much less their "stem" and their "leaf" nature); on the contrary, the new kind of ovary acquired an identity and a character of its own, and in that new identity and character the old identity and character of receptacle and carpel gradually melted away, and lost their distinctness, so that such an ovary has become a new member and is not simply a compound of receptacle and carpel. It is useless, therefore, to expect that such an ovary will build placentae, partitions, style, or stigma according to the rules in vogue with ordinary receptacle and carpel, and useless also to discuss whether in such an ovary the cavity is lined with carpel or not, for the ovarian wall is no longer either receptacle or carpel or both, it is ovarian wall; carpel and receptacle have not fused to form it; their tissue has melted away, so to speak, into the tissue which does form it. For simplicity I here treat this attainment of membership by such an ovary as if it were complete, though in fact it is not so in any ovary known to me, for in all of them some features of both carpel and receptacle may be traced, especially at top and bottom of the ovary. So also, with other parts of the flower; the placenta, which originated in the manner still shown by many flowers, as swollen edges of carpels, has become independent of its carpellary origin in many flowers, as in those with free central placenta, where no trace of

the old leaf nature may be found in its entire ontogeny. The tube of gamopetalous flowers is another structure which in some cases has attained to approximate independence, and the style and stigma yet another. All of these parts may become centers of independent (though usually limited) metamorphosis, altering in size, shape, number, building new structures (as the corona) all independently of anything they did before they acquired their present more or less completely independent membership. It is so with the ovule, originating in a macrosporangium, but now an independent member. The same is true of the embryo-sac, which, originating unquestionably as a germinated macrospore, has, after a long history, become a new member with a high, though not a complete independence. Some of its features are to be explained as a persistence of its ancient nature, but it is useless to attempt to interpret all its actions upon that basis, for it does some new things upon its own account—as a new member, the embryo-sac. To return for a moment to the flower as a whole, it is important to notice that the study of its morphology is in one sense complex and difficult, partly because it is a composite structure with various degrees of independence in its component parts, partly because its development in different families has been so independent that it has given rise to homoblastic rather than homogenetic homologies. Hence it is impossible to make distinct categories of members applying to all flowers, but each group must be considered by itself, a feature indeed which applies not to the flower alone but to the vegetative parts as well. Hence we must in theory recognize as potential members all organs, one may even say all recognizable parts, although in practice it is needful to take account for the most part only of those most conspicuous and distinct.

The realistic system, with its infinite gradations and limitless possibilities, is much harder to grasp and to apply, and is less pleasing to teach than the idealistic system, with its few distinct categories and their involved limitations. But it is truer to nature, more stimulating to research, and more replete with promise of great results.—W. F. GANONG, *Smith College, Northampton, Mass.*